

Aphyosemion pseudoelegans (Cyprinodontiformes: Nothobranchiidae), a new killifish species from the Cuvette centrale in the Congo Basin (Democratic Republic of Congo)

Rainer Sonnenberg^{1,2} & Jouke R. Van der Zee³

¹ Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany

² Max-Planck-Institut für Evolutionsbiologie, Department of Evolutionary Genetics, August-Thienemann-Strasse 2, D-24306 Plön, Germany. Corresponding author. E-mail: r.sonnenberg.zfnk@uni-bonn.de

³ Royal Museum for Central Africa, Vertebrate Section, Ichthyology, B-3080 Tervuren, Belgium.

Abstract. *Aphyosemion pseudoelegans*, new species, is described, based on collections that have been misidentified for decades as *A. elegans* by all authors. The new species superficially resembles *A. elegans*, but can be distinguished from the latter and all other species of the genus by a diagnostic combination of colour pattern characters, most prominently it has a dark red to black dorsal fin in males, a colour pattern always absent in all known *A. elegans* populations, including the type specimens, and an asymmetrical colour pattern on caudal fin margins versus symmetrical in *A. elegans*. *Aphyosemion pseudoelegans*, new species, is found in small rivers on the left bank of the middle Congo, where it occurs sympatric and sometimes even syntopic with *A. elegans*, *A. sp. aff. castaneum*, or an undescribed species of *Aphyosemion* at Ikela.

Résumé. *Aphyosemion pseudoelegans*, espèce nouvelle, est décrite, sur base de collections qui furent, depuis des décades, mal identifiées en tant que *A. elegans* par tous les auteurs. La nouvelle espèce ressemble superficiellement à *A. elegans*, mais peut en être distinguée, ainsi que de toutes les autres espèces du genre, par une combinaison diagnostique de caractères du patron de coloration. Principalement, elle présente une nageoire dorsale rouge foncé à noire chez les mâles, un patron de coloration toujours absent chez toutes les populations connues de *A. elegans*, y inclus les spécimens types, et un patron de coloration asymétrique des marges de la nageoire caudale alors qu'il est symétrique chez *A. elegans*. *Aphyosemion pseudoelegans*, espèce nouvelle, se rencontre dans de petites rivières de la rive gauche du Congo Moyen. Elle y est sympatrique, et parfois même syntopique, de *A. elegans*, *A. sp. aff. castaneum*, ou une espèce non-décrite de *Aphyosemion* à Ikela.

Key words. taxonomy, *Aphyosemion elegans*, DNA, morphology, distribution.

INTRODUCTION

In some recent publications, the taxonomy of species of *Aphyosemion s.l.* (Cyprinodontiformes: Nothobranchiidae) of the Congo basin was reviewed, leading to a revalidation of a taxon and the description of new species (Huber 1994, 2004, 2005a, b; Huber & Scheel 1981; Van der Zee & Huber 2006; Van der Zee & Sonnenberg 2010, 2011; Woeltjes 1984). Here the genus *Aphyosemion* Myers, 1924 is used in a more restricted sense, as proposed in three recent publications of the authors (Sonnenberg 2007; Van der Zee & Sonnenberg 2010, 2011). This corresponds with the subgenus *Aphyosemion* or the *A. elegans* species group of other authors (e.g. Collier 2007; Huber 2007; Murphy & Collier 1999; Wildekamp 1993) and includes 17 species currently accepted as valid (Van der Zee & Sonnenberg 2011). However, the species level taxonomy of this genus is still not settled. In a recent publication, the occurrence of another undescribed species was indicated, frequently misidentified as *A. elegans* (Baensch & Riehl 1985; Huber 2005 a, b; Ott 2002; Scheel 1968, 1990; Seegers 1997;

Van der Zee & Huber 2006; Wildekamp 1993) from the central Congo basin, based on diagnostic colour pattern differences and supported by a preliminary DNA study (Van der Zee & Sonnenberg 2011).

In 1899, Boulenger described *Haplochilus elegans* based on specimens which originated from Bikoro at Lac Tumba (Democratic Republic of Congo), and Coquilhatville, close to the Congo River (currently Mbandaka, capital of the province Équateur, Democratic Republic of Congo). Later this species was included in the genus *Aphyosemion*, erected by Myers in 1924.

Until recently, it was assumed that *A. elegans* is variable with respect to colour pattern, including that of the dorsal fin (Radda & Pürzl 1987; Huber 2004, 2005a, b; Van der Zee & Sonnenberg 2011; Wildekamp 1993). However, the known collections currently identified as *A. elegans* can easily be separated into two groups, distinguished by dorsal fin colouration and colour pattern of the caudal fin. One group has a light dorsal fin with many

small red dots and a symmetric colour pattern in the caudal fin, whilst the other has a mainly dark red dorsal fin (Van der Zee & Sonnenberg 2011) and an asymmetrical caudal fin pattern.

Within the description of *Haplochromis elegans*, a drawing of a male syntype was published, that clearly shows the colour pattern of the median fins. Additionally it was mentioned in the text, that all median fins are provided with carmine red dots (Boulenger 1899). A dark dorsal fin was never mentioned, nor does the drawing of a syntype show this character. This indicates that the types of *A. elegans* belong to the group with a narrow red edge and small red dots on a light background on the dorsal fin.

Aphyosemion elegans is widespread in the central and northern Congo Basin (Fig. 1). All known populations from the northern part of the basin have a dorsal fin with a narrow red edge and red dots on a light background. In contrast, in the central part of the basin, the Cuvette centrale, several populations show a complete or nearly complete dark red dorsal fin. Both phenotypes occur within the Cuvette centrale in sympatry, and at Bokuma (Équateur Province) they occur syntopic (Fig. 1; syntopic collection: MRAC 79229–79236 (*A. elegans*), MRAC 79237

(*A. pseudoelegans*, new species)). In addition, *A. pseudoelegans* can be found sympatric and syntopic with *A. sp. aff. castaneum* in parts of the Cuvette centrale and with an undescribed species of *Aphyosemion* at Ikela (see Van der Zee & Sonnenberg 2011; pers. obs. unpub.).

The probably first import of live specimens with dark red dorsal fins to Europe might have been made by Lambert in the sixties, originating from Boende (Baensch & Riehl 1985, as *A. elegans*). Both, *Aphyosemion elegans* sensu Boulenger (1899) and specimens with a dark red dorsal fin were kept and bred by aquarium hobbyists, especially the recent imports from the Boende area (Ott 2002; Van der Zee & Sonnenberg 2011), so it could be confirmed that the offspring only shows the parental colour pattern (pers. obs., H. Ott pers. comm.).

In addition, a recent phylogenetic analysis based on mitochondrial DNA data of 11 species of *Aphyosemion* indicated that specimens with a dark dorsal fin do not belong to *A. elegans*. Instead, they represent an undescribed species (Van der Zee & Sonnenberg 2011). In this paper the species with the dark dorsal fin, called preliminarily *A. sp. Cuvette* in Van der Zee & Sonnenberg (2011), is described as *Aphyosemion pseudoelegans*, new species.

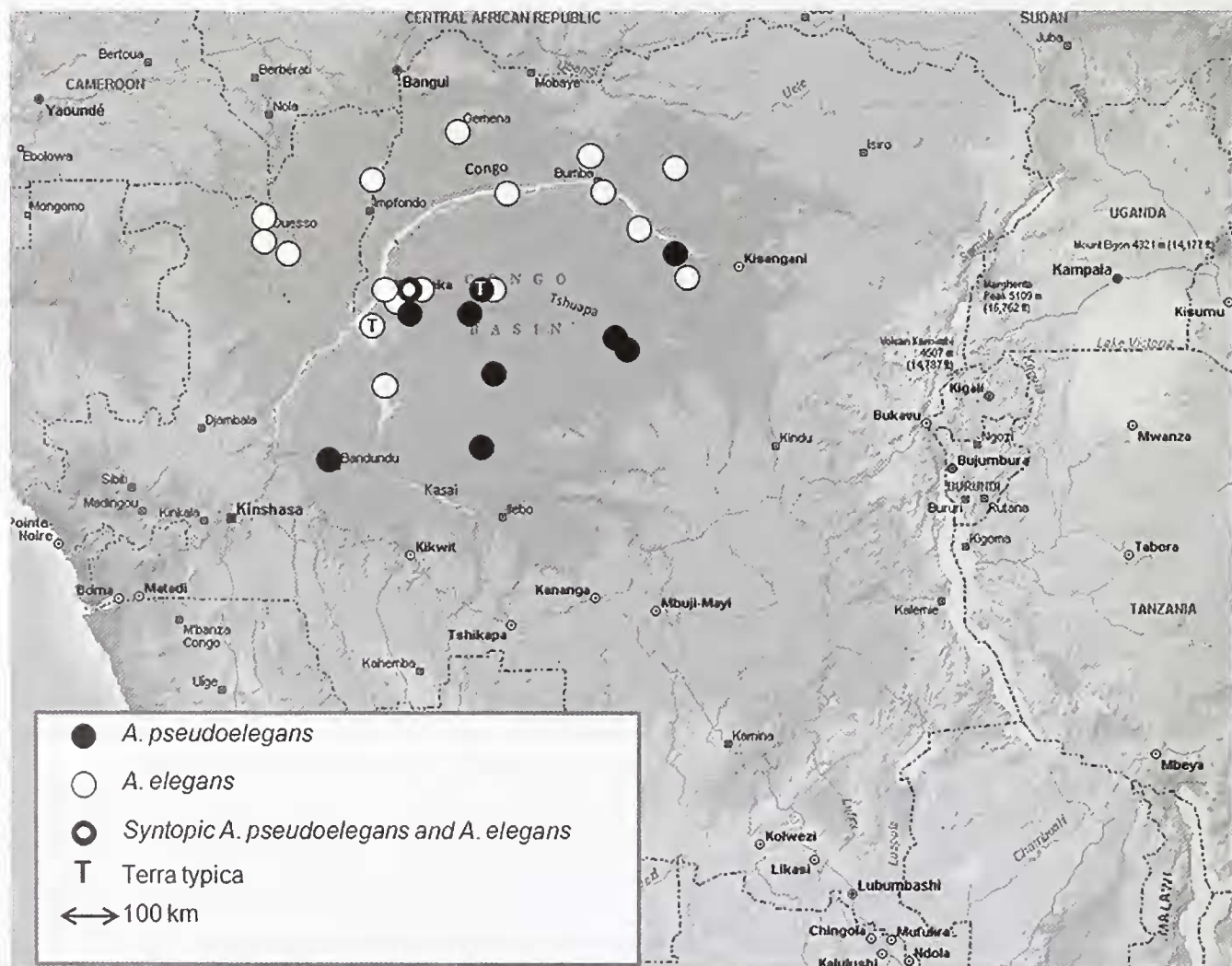


Fig. 1. Collection point map of *Aphyosemion pseudoelegans* and *Aphyosemion elegans* based on specimens and data from the AMNH, MNHN, MRAC, and ZSM collections.

Table 1. Morphometrics of *Aphyosemion pseudoelegans*, new species (H = holotype, P = paratypes: 8 males and 3 females). All measurements in percentages of standard length, standard length in mm. Paratype 1 MRAC 178017, paratypes 2–11 ZSM 32434.

	H ♂	P 1♂	P 2♂	P 3♂	P 4♂	P 5♂	P 6♂	P 7♂	P 8♂	P 9♀	P 10♀	P 11♀
Standard length	33.3	36.7	33.3	32.0	29.9	27.2	25.8	26.4	25.8	28.7	24.9	23.7
Body depth	18.0	19.1	18.0	17.5	19.7	19.8	20.5	20.1	20.5	19.5	21.1	21.1
Head length	22.5	21.8	21.0	22.5	22.7	22.1	22.1	23.1	22.1	20.6	22.8	22.8
Eye diameter	7.8	7.1	7.2	7.8	8.0	8.5	8.5	8.3	8.5	7.7	8.8	8.9
Interorbital width	10.2	10.6	11.1	10.9	10.7	12.1	12.4	10.6	12.4	10.5	10.4	11.4
Pre-dorsal length	69.1	68.1	66.4	68.1	67.2	68.8	69.4	65.2	69.4	65.9	69.1	70.9
Pre-anal length	54.7	59.4	55.0	55.6	53.8	57.3	57.8	57.2	57.8	53.7	53.4	57.8
Pre-ventral length	45.6	44.4	44.1	44.7	42.5	44.1	42.2	43.6	42.2	41.8	44.6	48.1
Dorsal fin base	12.3	12.0	10.8	9.7	12.0	11.0	11.0	11.0	10.9	9.4	10.4	10.1
Anal fin base	23.7	22.3	19.5	20.6	20.4	22.8	20.5	20.5	18.6	16.7	19.2	19.0
Caudal ped. length	23.7	22.6	23.1	22.5	24.1	22.8	23.9	21.6	25.2	23.3	18.9	22.4
Caudal ped. depth	12.3	12.5	13.2	12.2	14.0	13.6	13.6	13.3	13.2	12.2	12.9	13.5
Caudal ped. ratio	1.9	1.8	1.7	1.8	1.7	1.7	1.8	1.6	1.6	1.9	1.5	1.7

Table 2. Meristics of the types of *Aphyosemion pseudoelegans*, new species. Numbers indicate observed values, numbers in parentheses the frequency of occurrence; data of the holotype are indicated by an asterisk. Lateral line scale count only for the nine specimens with no loss of scales.

meristic count	number (frequency)
Dorsal fin rays	8 (7), 9 (5*)
Anal fin rays	13 (3), 14 (8*), 15 (1)
D/A	8 (4*), 9 (6), 10 (2)
Caudal fin rays	24 (3), 25 (5), 26 (2), 27 (1*), 28 (1)
Lateral line scales	29 (5), 30 (4*)

MATERIAL AND METHODS

The description of the new species is based on collections made in the Central Congo Basin, deposited in the Royal Museum for Central Africa (MRAC, Tervuren, Belgium) and the Zoologische Staatssammlung München (ZSM, Munich, Germany). Additional non-type and comparative material is listed in Van der Zee & Sonnenberg (2010, 2011) and below.

Counts and measurements follow Amiet (1987) and were taken with a digital caliper, partly under a dissecting microscope, and rounded to the nearest 0.1 mm. Measurements, including those taken on the head, were presented as percentages of standard length (SL). All visible fin

rays were counted, relative position of first dorsal fin ray to anal fin (D/A) is estimated as in Sonnenberg & Schunke (2010). Nomenclature for neuromast system on head follows Scheel (1968) and Van den Bergeijk & Alexander (1962), and for supraorbital (or frontal) squamation Hoedeman (1958). Heads of different species of *Aphyosemion* were scanned with a Scanco viva CT40 at the Max-Planck-Institut für Evolutionsbiologie (Plön, Germany). Digital X-ray images were made with a Faxitron LX-60 Digital Specimen Radiography System at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK, Bonn, Germany).

As species concept, we adopted the pragmatic approach by Moritz et al. (2000) which is similar to the Evolutionary or Phylogenetic Species Concept.

RESULTS

Aphyosemion pseudoelegans, new species (Fig. 2; Table 1–2)

Aphyosemion elegans, non (Boulenger, 1899): Baensch & Riehl (1985), Huber (2005 a, b), Ott (2002), Scheel (1968, 1990), Seegers (1997), Van der Zee & Huber (2006), Wilderkamp (1993).

Aphyosemion sp. Cuvette: Van der Zee & Sonnenberg (2011).

Aphyosemion sp. aff. *elegans*: Van der Zee & Sonnenberg (2011).



Fig. 2. A) Male of *Aphyosemion pseudoelegans*, collected at Boende in May 2002, not preserved. Digital copy of a colour slide. B) Female of *Aphyosemion pseudoelegans*, collected at Boende in May 2002, not preserved. Photographed by H. Ott three months after collection.

Holotype. MRAC 178016, male, 33.3 mm SL, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, 0°14'S, 20°50'E, coll. P. Brichard, 1969.

Paratypes. MRAC 178017, male, 36.7 mm SL, collected with the holotype; ZSM 40762 (ex ZSM 32434), 7 males, 25.8–33.3 mm SL, 3 females, 23.7–28.7 mm SL, Democratic Republic of Congo, Bandundu Province, Lokoro Basin, Lui Kotale, 2°45'S, 20°21'E, coll. G. Hohmann, November 2000.

Diagnosis. (Figs 2–3) *Aphyosemion pseudoelegans* shows the diagnostic combination of characters for the genus *Aphyosemion*, which are: preopercular neuromast system with six pores, slender body shape, posterior origin of dorsal fin, dorsal fin small with less than ten fin rays, extend-

ed fin rays at the edges of the caudal fin in males, and females with a well visible reticulation due to dark scale borders.

Males of *A. pseudoelegans* differ from all other *Aphyosemion* species by a diagnostic combination of colouration characters. Most prominently it differs from all other species except *A. congium* (Ahl, 1924) by the almost complete dark red to black dorsal fin versus red dots or stripes on lighter background. It also differs from all other species except *A. elegans* (Fig. 4) by irregular narrow vertical red bars, based on confluent dots, on flanks of males.

It differs from *A. congium* by having an asymmetrical colour pattern of the marginal and submarginal bands in the caudal fin versus colour pattern of dorsal and ventral marginal and submarginal bands symmetrically.



Fig. 3. Dorsal fin of male specimens preserved in ethanol. In these specimens the red pigmentation is lost, but the difference in colour pattern between the two species is still visible. **A)** *A. pseudoelegans*, MRAC 80709–80777, Bokuma, with plain greyish to brownish fin tissue. **B)** *A. elegans*, MRAC 93724, Bokuma, fin tissue with light dots which are the remains of the former red pigmentation.

Aphyosemion congicum has only a few red dots on the flanks and an almost dotless anal fin versus many red dots or bars on flanks, anal fin with many red dots or inter radial red stripes.

Besides the dark dorsal fin, the body colour pattern resembles that of *A. elegans*, but *A. pseudoelegans* has an asymmetric colour pattern in the caudal fin versus a symmetric pattern in *A. elegans*. In general, *A. pseudoelegans* is more intensely pigmented than *A. elegans*, often having larger and more red dots on the flanks and a denser red pigmentation of the head. *Aphyosemion elegans* always shows two or more small isolated rounded red dots underneath the eye, whereas in most *A. pseudoelegans* these dots are larger and irregular and often fused, forming a red streak. In very heavily pigmented *A. pseudoelegans*, the red dots in the caudal fin may form vertical bars; this is never the case in *A. elegans*.

Both species may show narrow vertical dark red bars on the flanks, but in *A. elegans* these bars may run all over the flanks, whereas in *A. pseudoelegans* these bars in most cases only cover the ventral part of the flanks, and dorsally frequently with nearly regular rows of red dots.

Description. See Figures 2–3 for general appearance and colour pattern, Table 1 for morphometric, and Table 2 for meristic data of the type series. *Aphyosemion pseudoelegans* is a slender, elongate species. It shows strong sexual dimorphism, males more colourful, unpaired fins larger and with fin extensions. Relatively large species within *Aphyosemion* (up to 51.4 mm TL), laterally slightly compressed; dorsal profile slightly convex, greatest body depth approximately anterior or at pelvic fin insertion. Ventral profile slightly convex from head to end of anal fin, straight or slightly concave on caudal peduncle. Caudal peduncle slender, peduncle depth is 1.5–1.9 times in length.

Snout slightly rounded, mouth directed upwards, lower jaw longer than upper jaw. Dentary with outer row of large and inner irregular rows of smaller unicuspid, curved teeth; premaxilla with some larger and several smaller unicuspid and curved teeth.

Frontal (after Scheel, 1968) or nasal (after van Bergeijk & Alexander, 1962) neuromasts in separate grooves, preopercular canal with six pores.

Scales cycloid, entirely scaled except ventral surface of head; frontal squamation of G-type; scales on mid-longi-



Fig. 4. **A)** Male of *Aphyosemion elegans*, commercial import (2006) from the Tshuapa River near Boende, not preserved. **B)** Female *Aphyosemion elegans*, commercial import (2006) from the Tshuapa River near Boende, not preserved. Photographed by H. Ott.

tudinal series 28–30, with two scales posterior to hypural plate; seven transversal scales, 12 scales around caudal peduncle.

Small dorsal fin with 8–9 fin rays, first dorsal fin ray inserts above 8–10th anal fin ray; anal fin with 13–15 rays; posterior dorsal and anal fin rays slightly elongated in males; caudal fin with 24–28 rays, with extensions on upper and lower fin rays.

X-ray images of three males from comparative material (MRAC 37840–843) show 29–30 vertebrae and well separated upper and lower hypural bones.

Live colouration. Males (Fig. 2A). Flanks golden to brown, with yellow to bluish-green iridescence. Most flank scales with a red dot. These dots are mainly situated at the posterior edge of the scales and usually form up to five

parallel, interrupted stripes. Many populations have in addition scales that have the red dots situated at the anterior edge of the scale. This causes, in combination with the adjacent scales above and below with red dots at the posterior edge, vertical narrow red bars. Three red streaks on opercle in an approximate 45° angle. One or two infra-buccal bands present on the lower jaw. Red dots underneath the eye often united in a red streak. Pectoral fin translucent yellow to orange with a whitish or light yellow edge; red dots present, sometimes concentrated near the yellow edge forming a red band. Anal fin light blue or light yellow, provided with many red dots and/or inter-radial red stripes, sometimes with a yellow or light blue margin. Dorsal fin predominantly dark red to almost black, with a narrow light band at the base and edged with a white, yellow, blue or nearly black band, depending on ex-

posture to light. Central part of caudal fin with many red dots and/or inter-radial stripes. Upper margin yellow or whitish to light blue, sub-marginal band dark red, lower margin with broad light sub-marginal band and narrow dark red marginal band. In some populations, including the types, this red band is interrupted or absent.

Females (Fig. 2B). Flanks grey with strong red reticulation; red streaks on opercle reduced, often only middle streak clearly visible; infra-buccal band absent. All fins transparent; edge of anal fin and distal part of ventral fin light blue or white; small red dots on anal fin, large red dots and/or short inter-radial stripes in dorsal fin; small red dots on anterior dorsal edge and at base of caudal fin.

Colour in ethanol. The types from Boende and the comparative material from Bokuma show the typical pattern of preserved *Aphyosemion* species, in which the red pigmentation pattern, after preservation in formalin and transfer into ethanol, leaves corresponding patterns of lighter areas than the body colouration (Van der Zee & Sonnenberg 2010). The dark red band in the dorsal fin becomes nearly black, grey, or dark brown. After eleven years in 96% ethanol the red colour of the ZSM paratypes is still present and resembles the live colour pattern except for the iridescence and the dark red band in the dorsal fin and upper caudal fin that became nearly black. This is also the case in one collection originating from Boende and two of four collections coming from Ikela. Material collected here in 1958 and 1972 has the red pigmentation perfectly preserved, whereas material collected in 1955 and 1959 shows the typical colouration of preserved *Aphyosemion* specimens. Interestingly, the colouration of the formerly dark red dorsal in *A. pseudoelegans* leaves, when preserved in ethanol, a darker area than the red pigment on the body; whereas red pigment on the body and dorsal fin leaves lighter areas in *A. elegans* (see Fig. 3). Eventually the red pigment of the dorsal fin differs or the colour is based on a combination of the more common red pigment as in other species and a darker pigment, which becomes nearly black and later greyish in preservation.

Habitat and Distribution. Like all members of the genus *Aphyosemion*, *A. pseudoelegans* inhabits shallow and small brooks under forest cover. Currently known collections indicate, that *A. pseudoelegans* is restricted to tributaries on the left bank of the middle Congo basin, also known as the Cuvette or Cuvette centrale. This area is enclosed by the Congo River in the north, east, and west, and by the Kasai River in the south of the Democratic Republic of Congo (Fig. 1). *Aphyosemion pseudoelegans* is present in the Tshuapa, Lomani and Lokoro drainages.

Etymology. The name *Aphyosemion pseudoelegans* refers to the misidentification as *A. elegans*, a similar species, but lacking the typical dark red dorsal fin and the

asymmetric caudal fin colour pattern; from the Greek ψευδής, meaning lying or false, the latter is our intended translation.

DISCUSSION

The study of the killifishes of the Congo Basin by the senior author indicates, that there are still several undescribed species in museum collections and the collections made recently indicate, that further undescribed species are still to be discovered in this large and mostly not well sampled part of Africa (see also Sonnenberg et al. 2011, Van der Zee & Sonnenberg 2010, 2011).

We recently made the assumption that *A. elegans* and *A. pseudoelegans* represent different species (Van der Zee & Sonnenberg 2011). Both were kept and bred by killifish hobbyists for several years and their observations indicate that *A. pseudoelegans* is not simply a case of polychromy of *A. elegans*, which is supported by recently published DNA data (Van der Zee & Sonnenberg 2011). In addition, we did not find any indication of potential hybrids in the studied material of both species. The diagnosis of *A. pseudoelegans* from *A. elegans* is mainly based on colour pattern differences of unpaired fins. In general, this genus has a comparatively high variability in colouration (see also Van der Zee & Sonnenberg 2011), but beside details, the general pattern of fins, especially the order of dark and light marginal and submarginal bands is a comparatively stable character according to our observations. *Aphyosemion elegans* and *A. pseudoelegans* can easily be distinguished by their different, stable pattern of light and dark areas, and less by their similar, but not identical, body colour pattern, which in addition can also be variable between different populations of a species. For nothobranchiids it is assumed that male colouration is important for female mate choice within and between species (Amiet 1987; Brosset & Lachaise 1995; Kullmann & Klemme 2007) and Van der Zee et al. (2007) presume that especially the colour pattern of the caudal peduncle and unpaired fins might have an important role.

With the description of *A. musafirii* we presented a preliminary mtDNA analysis for some species of *Aphyosemion*, including *A. pseudoelegans* (Van der Zee & Sonnenberg 2011). We indicated an incongruence of mtDNA results and phenotype within the samples of the Cuvette centrale. This is also true for the *A. pseudoelegans* samples, which were labelled within this phylogeny (Van der Zee & Sonnenberg 2011, fig.9) as *A. sp. Cuvette* (sample RS1019) or *A. sp. aff. elegans* (samples RS1508 & RS1509). These samples turn out in different parts of the phylogeny, but are grouped together in a preliminary analysis of a fragment of the nuclear LSU (unpublished data). Additionally, a population originating from Bandundu belongs to *A. pseudoelegans* according to

its phenotype with the diagnostic dark red dorsal fin. This is well visible on available pictures and specimens deposited in the MRAC from a collection in 1982. However, the published mtDNA cytochrome b sequence (Murphy & Collier 1999, as *Aphyosemion cognatum*) deviates from any of our sequences (results not shown).

Due to some incongruencies between mtDNA, nuclear DNA, and phenotype we hesitate at the moment to discuss the phylogenetic position of the different species and the cause of such incongruencies, until further samples and DNA data are available. A potential cause for incongruencies can be mitochondrial introgression, which we discussed in the recent publication (Van der Zee & Sonnenberg 2011) and which is known to occur in the nothobranchiid genus *Chromaphyosemion* (Sonnenberg 2007). But in the case of incongruent DNA and phenotype data, it has to be considered that also nuclear DNA and mtDNA can be affected. An example of homogenization of nuclear rRNA genes in F1 hybrids is given by Wang et al. (2010). This would make it impossible to detect such crosses, which usually is possible with nuclear sequence data (see e.g. Sonnenberg et al. 2007). In addition, hybrid speciation as in some African cichlids (Schliewen & Klee 2004; Schwarzer et al. 2011) might also not be excluded, especially as the species involved are in contact within the Cuvette centrale. The available data indicate a complex pattern within the *Aphyosemion* of the Congo Basin, and more data will be necessary to understand the evolution and phylogeography of these fishes (Van der Zee & Sonnenberg 2011).

Currently, it appears that *A. pseudoelegans* is restricted to the Cuvette central on the left bank of the Congo, whereas *A. elegans* is also found further north and on the right bank of the Oubangui in the Republic of Congo, but not in the south and southeast of the Cuvette (Fig. 1). Their distribution areas overlap at least in the region of the lower Tshuapa River, where they can occur in sympatry or close parapatry, e.g. around Boende (Fig. 1). *Aphyosemion pseudoelegans* can also be found in syntopy with other *Aphyosemion*, e.g. at Ikela with an undescribed species only known from preserved specimens in the MRAC, and near Lui Kotale with *A. sp. aff. castaneum* (see Van der Zee & Sonnenberg 2011).

COMPARATIVE AND ADDITIONAL NON-TYPE MATERIAL

Aphyosemion elegans (Boulenger, 1899): MRAC 990–992, Syntypes, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bikoro, coll. P. Delhez, no year; MRAC 993, Syntype, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Coquilhatville (present Mbandaka), coll. P. Delhez, no year; MRAC 1488, Democratic Republic of Congo, Uélé (not specified), coll. A. Hutereau, 5.I.1905; MRAC 21628, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. Van Oye, 2.V.1923; MRAC 21636–639, Democratic

Republic of Congo, Orientale Province, Mondimbi, coll. J. Ghesquière, XI.1927; MRAC 21642–648, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. Van Oye, 2.V.1923; MRAC 21649–653, Democratic Republic of Congo, Orientale Province, Mondimbi, coll. J. Ghesquière, XI.1927; MRAC 21670–682, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. Van Oye, 2.V.1923; MRAC 21683–697, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. Van Oye, 2.V.1923; MRAC 23539–546, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. Van Oye, 2.V.1923; MRAC 44888–894, Democratic Republic of Congo, Équateur Province, Sources à Gemena, coll. P. Henrard, 1935; MRAC 45973–999, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. J. Ghesquière, IV.1936; MRAC 46000–46049, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Eala, coll. J. Ghesquière, IV.1936; MRAC 72763, Democratic Republic of Congo, Orientale Province, Buta, coll. J. Hutsebaut, 1949; MRAC 79229–79236, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, VII.1952; MRAC 80778–80780, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, 1952; MRAC 93724–93773, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, III.1954; MRAC 96831–841, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bonguma 8 km S of Bokuma, coll. P. Lootens, 1952; MRAC 98696–699, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bonguma, coll. P. Lootens, 1955; MRAC 73-23-P-11233–302, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. R. Philippe, VIII.1956.

Aphyosemion pseudoelegans: AMNH 1-252189, Democratic Republic of Congo, Équateur Province, riv. Ta'Simon a Boaugi, coll. R. Monsembula, 23.V.2010; MRAC 21634–635, Democratic Republic of Congo, Équateur Province, Flandria, coll. G. Hulstaert, IV.1928; MRAC 30113, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 15.IV.1930; MRAC 30123, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 15.IV.1930; MRAC 30130–134, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 18.X.1931; MRAC 30203–211, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 16.IV.1931; MRAC 30222–259, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 1931; MRAC 37840–843, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Flandria, coll. G. Hulstaert, 15.VII.1931; MRAC 47823–830, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Flandria, coll. G. Hulstaert, 1936; MRAC 72531–545, Democratic Republic of Congo, Équateur Province, riv. Ilolo, Flandria, coll. G. Hulstaert, 13.II.1948; MRAC 79237, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, VII.1952; MRAC 79908–909, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, 10.VII.1952; MRAC 80709–80777, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, 1952; MRAC 96830, Democratic Republic of Congo, Équateur Province, Banguna a 8 km Sud de Bokuma, coll. P. Lootens, 1954; MRAC 96688–693, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Bokuma, coll. P. Lootens, I.1954; MRAC 98700–701, Democratic Republic of Congo, Orientale Province, Tshuapa River, Ikela, coll. P. Lootens,

15.IV.1955; MRAC 99000, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Marais de la Kea, Boende, coll. R. Philippe, IV.1955; MRAC 99753, Democratic Republic of Congo, Équateur Province, riv. Momboyo, Losclinga, coll. G. Hulstaert, 5.V.1955; MRAC 99746–752, Democratic Republic of Congo, Riv. Loc, unknown location, coll. G. Hulstaert, 16.V.1955; MRAC 101891–915, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, marches around Boende, coll. R. Philippe, VII.1955; MRAC 131305–311, Democratic Republic of Congo, Orientale Province, Tshuapa River, Losaka stream, Ikela, coll. H. Matthes, 9.IX.1959; MRAC 175812–842, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. P. Lootens, II.1966; MRAC 178018–023, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. P. Brichard, 1969; MRAC 73-23-P-11040–42, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. R. Philippe, 1956; MRAC 73-23-P-11043–232, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. R. Philippe, VI.1956; MRAC 73-23-P-11303–542, Democratic Republic of Congo, Équateur Province, Tshuapa Basin, Boende, coll. R. Philippe, IX.1956; MRAC 75-35-P-37–40, Democratic Republic of Congo, Orientale Province, district Ikela, Yetsi, coll. P. Lootens, VI-II.1972; MRAC 79-09-P-732–740, Democratic Republic of Congo, Orientale Province, Ikela territory, Yayama, coll. J. Lambert, 17.V.1958; MRAC 84-25-P-3, Democratic Republic of Congo, Équateur Province, Boteka, coll. P. Lootens, I.1984; MRAC 85-47-P-1–4, Democratic Republic of Congo, Bandundu Province, Kasai drainage, Bandundu, coll. K. Klute, X.1982; MRAC 2010 Congo Expedition, Location 66, stream near Lieki opposite Yangambi, coll. J. Snoeks & E. Vreven, 27.V.2010.

Acknowledgements. The authors wish to thank the following persons for their help in realizing this paper: H. Ott (Mönchengladbach, Germany) for providing pictures and specimens of *A. pseudoelegans* and *A. elegans*; M. Stiassny for providing a picture and a drawing of *A. pseudoelegans* present in the AMNH (New York, USA) collection, D. Neumann and U. Schliewen (ZSM, München, Germany) for loan of specimens under their care and providing data and photos; M. Parrent, J. Snoeks, and E. Vreven (MRAC, Tervuren, Belgium) for support and access to the collections under their care, M. Parrent in addition for the translation of the abstract into French, F. Herder (ZFMK, Bonn, Germany) for access to the digital X-ray machine, D. Tautz (MPI, Plön, Germany) for access to the micro Computer Tomograph, and A.C. Schunke (MPI, Plön, Germany) for help with earlier versions of the manuscript. In addition, we are grateful for the critical comments of two anonymous reviewers.

REFERENCES

- Ahl E (1924) Über neue afrikanische Zahnkarpfen der Gattung *Panchax*. Zoologischer Anzeiger 60: 303–312
- Amiet JL (1987) Le Genre *Aphyosemion* Myers (Pisces, Teleostei, Cyprinodontiformes). Faune du Cameroun, Volume 2. Sciences Nat, Compiegne, France
- Baensch HA & Riehl R (1985) Aquarien-Atlas. Band 2. Mergus Verlag, Melle, Germany
- Boulenger GA (1899) Matériaux pour la fauna du Congo. Poissons nouveaux du Congo. Cinquième Partie. Cyprins, Silures, Cyprinodontes, Acanthoptérygiens. Annales du Musée du Congo (Série Zoologie) Volume 1 (fasc. 5): 97–128, pls. 40–47
- Brosset A, Lachaise D (1995) Evolution as a lottery conflicting with evolution via sexual selection in African rainforest-dwelling killifishes (Cyprinodontidae, Rivulinae, *Diapteron*). Evolutionary Biology 28: 217–264
- Collier GE (2007) The genus *Aphyosemion*: Taxonomic history and molecular phylogeny. Journal of the American Killifish Association 39: 147–168
- Hocdeman J (1958) The frontal scalation pattern in some groups of toothcarps (Pisces: Cyprinodontiformes). Bulletin of Aquatic Biology 1: 23–28
- Huber J-H (1978) Contribution à la Connaissance des Cyprinodontidés de l'Afrique Occidentale: Caractères taxonomiques et Tentative de Groupement des Espèces du genre *Aphyosemion* (Cyprinodontidés). Revue française d'Aquariologie et Herpétologie 5: 1–29
- Huber J-H (1994) *Aphyosemion passaroii*, espèce inédite du Gabon sud-oriental, au patron de coloration unique et description complémentaire de *Aphyosemion decorsei* (Pellegrin). Cyprinodontiformes, Aplocheilidae. Revue française d'Aquariologie 20: 77–80
- Huber J-H (2004) Description of a new *Aphyosemion* species from Congo, *A. plagitaenium* n. sp., exhibiting a probable intra-generic color convergence with oblique bars. Freshwater and Marine Aquarium 27: 70–74
- Huber J-H (2005a) Identifikation einer kleinen Sammlung von *Aphyosemion* aus Zaire im Münchener Museum (Z.S.M.), mit weiteren Kommentaren über die Validität der bekannten Komponenten der *elegans*-Superspezies. 1. Teil. Deutsche Killifisch Gemeinschaft Journal 37: 8–21
- Huber J-H (2005b) Identifikation einer kleinen Sammlung von *Aphyosemion* aus Zaire im Münchener Museum (Z.S.M.), mit weiteren Kommentaren über die Validität der bekannten Komponenten der *elegans*-Superspezies. 2. Teil. Deutsche Killifisch Gemeinschaft Journal 37: 35–45
- Huber J-H (2007) Killi-Data 2007. Updated checklist of taxonomic names, collecting localities and bibliographic references of oviparous cyprinodont fishes (Atherinomorpha, Pisces). Société française d'Ichthyologie, Paris (German edition)
- Huber J-H, Scheel JJ (1981) Revue systématique de la super-espèce *Aphyosemion elegans*. Description de *A. chauchei* n.sp. et *A. schioetzi* n. sp. Revue française d'Aquariologie 8: 33–42
- Kullmann H, Klemme B (2007) Female mating preference for own males on species and population level in *Chromaphyosemion* killifishes (Cyprinodontiformes, Nothobranchiidae). Zoology 110: 377–386
- Moritz C, Patton JL, Schneider CJ, Smith TB (2000) Diversification of rainforest faunas: an integrated molecular approach. Annual Reviews in Ecology and Systematics 31: 533–563
- Murphy WJ, Collier GE (1999) Phylogenetic Relationships of African Killifishes in the Genera *Aphyosemion* and *Fundulopanchax* inferred from Mitochondrial DNA Sequences. Molecular Phylogenetics and Evolution 11: 351–360
- Myers GS (1924) A new poeciliid fish from the Congo, with remarks on funduline genera. American Museum Novitates 116: 1–9
- Ott H (2002) Endlich wieder da: *Aphyosemion elegans*. Deutsche Killifisch Gemeinschaft Journal 34: 173–176
- Radda AC, Pürzl E (1987) Colour Atlas of Cyprinodonts of the Rain Forests of Tropical Africa. Hofmann Verlag, Wien
- Scheel JJ (1968) Rivulins of the Old World. TFH Publications, New Jersey
- Scheel JJ (1990) Atlas of the Killifishes of the Old World. TFH Publications, New Jersey

- Schliewen UK, Klee B (2004) Reticulate sympatric speciation in Cameroonian crater lake cichlids. *Frontiers in Zoology* 1: 5, 12 pp.
- Schwarzer J, Misof B, Schliewen UK (2011) Speciation within genomic networks: a case study based on *Steatocranus* cichlids of the lower Congo rapids. *Journal of Evolutionary Biology* 25: 138–148
- Seegers L (1997) Killifishes of the World. Old World Killies I. Aqualog, A.C.S. GmbH, Morfelden-Walldorf
- Sonnenberg R (2007) Description of three new species of the genus *Chromaphyosemion* Radda, 1971 (Cyprinodontiformes: Nothobranchiidae) from the coastal plains of Cameroon with a preliminary review of the *Chromaphyosemion splendopleure* complex. *Zootaxa* 1591: 1–38
- Sonnenberg R, Nolte AW, Tautz D (2007) An evaluation of LSU rDNA D1–D2 sequences for their use in species identification. *Frontiers in Zoology* 4:6, 12 pages
- Sonnenberg R, Schunke AC (2010) On the taxonomic identity of *Fundulus beauforti* Ahl, 1924 (Cyprinodontiformes, Aplocheiloidei). *Zoosystematics and Evolution* 86: 337–341
- Sonnenberg R, Woeltjes T, Van der Zee JR (2011) Description of *Fenerbahce devosi* (Cyprinodontiformes: Nothobranchiidae), a new species of dwarf killifish from the eastern Congo Basin in the Democratic Republic of Congo. *Zootaxa* 2966: 1–12
- Van Bergeijk WA, Alexander S (1962) Lateral line canal organs on the head of *Fundulus heteroclitus*. *Journal of Morphology* 110: 333–346
- Van der Zee JR, Huber J-H (2006) Zur Identität von *Aphyosemion christyi* (Boulenger, 1915), *Aphyosemion schoutedeni* (Boulenger, 1920) und *Aphyosemion castaneum* Myers, 1924. (Pisces, Cyprinodontiformes, Aplocheilidae). *Deutsche Killifisch Gemeinschaft Journal* 38: 131–142
- Van der Zee JR, Sonnenberg R (2010) *Aphyosemion teugelsi* (Cyprinodontiformes: Nothobranchiidae), a new species from a remote locality in the southern Democratic Republic of the Congo. *Zootaxa* 2724: 58–68
- Van der Zee JR, Sonnenberg R (2011) *Aphyosemion musafirii* (Cyprinodontiformes: Nothobranchiidae), a new species from the Tshopo Province in the Democratic Republic of Congo, with some notes on the *Aphyosemion* of the Congo Basin. *Bonn zoological Bulletin* 60: 73–87
- Van der Zee JR, Woeltjes T, Wildekamp RH (2007) Aplocheilidae. Pp. 80–240 in: Stiassny MLJ, Teugels GG, Hopkins CD (eds.) *The Fresh and Brackish Water Fishes of Lower Guinea, West-Central Africa*. Volume II. IRD Éditions, Paris
- Wang S, Zhang L, Hu J, Bao Z, Liu Z (2010) Molecular and cellular evidence for biased mitotic gene conversion in hybrid scallop. *BMC Evolutionary Biology* 10:6, 10 pages
- Wildekamp RH (1993) *A World of Killies*. Atlas of the Oviparous Cyprinodontiform Fishes of the World. Volume 1. The American Killifish Association, Mishawaka, Indiana
- Woeltjes T (1984) *Aphyosemion lefiniense* spec. nov. (Pisces, Atheriniformes, Rivulinae) aus dem Lefini Subsystem des Kongo-Flusses in der Volksrepublik Kongo. *Deutsche Killifisch Gemeinschaft Journal* 16: 3–14